

Simultaneous flowering of umbrella bamboo (*Fargesia murielae*) at its native home in Central China

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Abstract: Flowering pattern and seedling establishment of umbrella bamboo (*Fargesia murielae* (Gamble) Yi) were studied in its native habitat, Mount Shennongjia in Central China. Here in 1996–2000, over 95% of the bamboo plants simultaneously flowered and died, extending from lower elevations to the higher mountains along the altitude and from southwest to northeast along the mountain settings. Bamboo seedlings emerged after the simultaneous flowering, achieving an average density of 5 460 seedlings·m⁻² in the autumn of the year following the flowering. After a high mortality throughout the first winter, bamboo seedlings remained a stable density in following 2–4 years (1130–1230 seedlings·m⁻²). Seedling density positively related to the coverage of parent bamboo, but negatively to the herb layers.

Key words: Altitudinal scale, bamboo sites, flowering pattern, seedling establishment, Shennongjia.

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Introduction

The life history of many bamboo species is characterized by an unusual flowering habit. They often flower and die simultaneously over wide areas at long intervals (3–120 years), and then regenerate from seed or rhizome (Janzen 1976; Liese 1985; Campbell 1985; Young 1985; Taylor *et al.* 1988, 1991, 1993; Abe *et al.*, 2001). Physiological and genetic factors involved in inducing the simultaneous flowering of the bamboo are unknown to date (Gielis *et al.* 1999; Liese 2001), but several hypotheses exist concerning the causes of flowering. One explanation is that of external controls on physiological processes by available resources such as rainfall (Campbell 1991). Another is a widely accepted theory proposed by Janzen (1976), which assumes that irregular fruiting cycles are sufficient disequilibria to inhibit seed predators from maintaining populations large enough to decimate a “mast year” of fruiting. Recently, Keeley and Bond (1999, 2001) proposed a “fire cycle hypothesis”, arguing that lightning-ignited wildfire has synchronized flowering by creating the conditions for monocarpic reproduction of clones at long intervals and delaying of reproduction. However, all these hypotheses lack of field evidence. One reason is that the flowering cycle of many bamboo species may be 30–70 years or more, longer than the active professional life of an individual researcher, so that one person does not usually have the opportunity to observe a full cycle or conduct relevant experiments. Therefore, recording the flowering of particular species is an essential aspect for understanding the bamboo flowering behavior.

Umbrella bamboo (*Fargesia murielae* (Gamble) Yi, Poaceae) is one of the most popular and widely grown bamboos in the

colder areas of Europe and North America (Eberts 1996; Keng and Wang 1996). It is a native Chinese bamboo endemic to Mount Shennongjia in western Hubei of Central China (Li 1996; Keng and Wang 1996; Li 2003). In Europe and North America, umbrella bamboo gregariously flowered and died in 1993–1998 (Renvoize 1993; Eberts 1996; Gielis *et al.* 1999); this was the first flowering since 1907 when the species was recorded by Ernest Wilson (Sargent 1911; Eberts 1996; Shannik 1999). On Mount Shennongjia, umbrella bamboo also flowered in the 1990s, which provided a rare opportunity for observing the flowering pattern and seedling establishment of this species.

Materials and methods

Study area

Mount Shennongjia (N31°18'–31°52', E109°58'–110°58'), located at western Hubei in Central China (Fig. 1), comprises 3 200 km² of steep rugged mountains and elevations that range from 400 to 3 100 m asl. The extreme topographic relief coupled with the elevational range provides habitats for 2 762 species of vascular plants, and climatic conditions that extend from warm temperate through boreal (Ban *et al.* 1995; Zhu and Song 1999). Umbrella bamboo occurs in the upper mountains above 2400 m until the mountaintop of 3 100 m (Li 2003). In this altitudinal section, the annual precipitation ranges from 2 200–2 700 mm and mean annual temperatures from 1–4 °C. Umbrella bamboo usually grows in the forests as a dense understorey; however, it also survives in the degraded habitats such as in open shrubs and mountainous meadows. Because of the high elevation, the bamboo stands are usually subject to strong, cold winter winds so that the associated vegetation is characterized by plants that have a cold-temperate affinity. In the bamboo habitats at lower elevations (2 400–2 700 m), farges fir (*Abies fargesii* Franch.) co-occurs with broadleaved deciduous trees such as *Betula albo-sinensis* Burk., *Acer mono* Maxim. and *Popula davidiana* Dode, forming mixed forests. On the upper habitats (2700–3100 m), broadleaved trees give way to *A. fargesii*, forming a pure coniferous forest.

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Field investigation

Field investigations were conducted from June 2000 to July 2001 in the bamboo habitats, which geographically fall in the Shennongjia National Nature Reserve. Features of bamboo flowering, structures of bamboo-associated vegetation, and density of bamboo seedlings were surveyed along three mountain paths across the umbrella bamboo ranges inside the reserve (Fig. 1). Path 1 (16 km) was from the northern-east boundary of the reserve (Yaziko, N31°30'920", E110°20'127", alt. 1820 m) to the mountain peak (Observation Tower, N31°27'069", E110°16'040", alt. 2930 m), representing the flowering pattern on the northern slopes. Path 2 (21 km) was from the southern-west boundary (Gangou, N31°17'611", E110°09'720", alt. 1250 m) towards the Observation Tower, representing the flowering pattern on the

southern slopes. Path 3 (12 km) was from the Monkey Stone (N31°27'403", E110°12'039", alt. 2530 m) to the South Gate (N31°25'190", E110°10'413", alt. 2680 m), representing the flowering pattern along the mountain ridges. In all, 62 sites were surveyed along the three paths, at intervals of about 300 m across the bamboo distribution range. The location of each site was recorded by a handy GPS receptor. In each site, a quadrat (area varied from 20–200 m²) was set up and the underlying plant community classified into community types following Ban *et al.* (1995): (1) conifer - bamboo community, (2) deciduous broad-leaved tree - bamboo community, (3) pure bamboo community, (4) shrub - bamboo community, and (5) bamboo - meadow community. The dominant species were recorded and %-cover was estimated for each storey (i.e., canopy layer, bamboo layer, and herb layer).

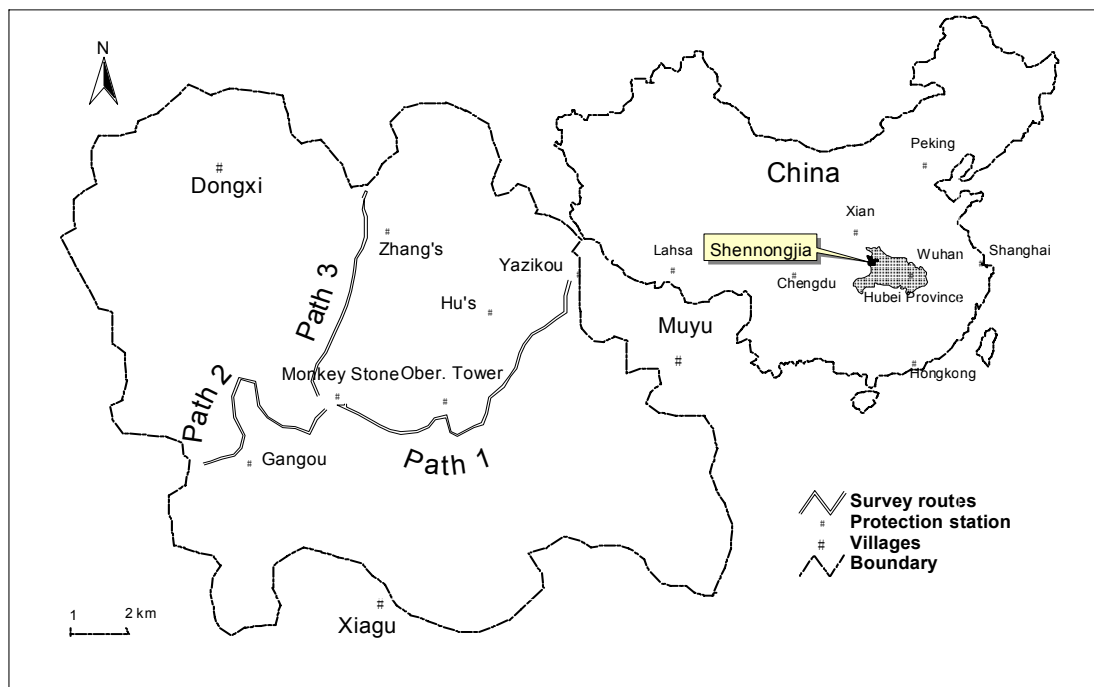


Fig. 1 Location of Mount Shennongjia and survey paths in the Shennongjia National Nature Reserve, Central China

In each quadrat, several 1 m × 1 m sub-quadrats were set up to exam the flowering year of the bamboo. Two criteria were applied to determine the flowering year: one based on the appearance of parent culms and the other based on the number of culmlets of the bamboo seedlings. The parent culms in the first year after simultaneous flowering still had intact branches, complete inflorescences, and a fresh yellow color; in the second year, inflorescences withered, branches were yellowish-dark and broken, culms darkish-yellow; and in the third year, most of the branches decayed, and culms were dark. However, it is very difficult to determine the age of the culms after three years. Qin *et al.* (1989, 1993) recommended another way to determine the flowering year of the parent bamboo: *Fargesia* bamboo seeds tend to germinate synchronously in the first year after flowering. Thereafter, a seedling usually produces one new culmlet each year from the rhizome base in its young phase (up to 5–7 years of age). Thus, counting the culmlets of the seedlings can deduce the flowering year of their parent culms. Surveys on bamboo

seedlings were conducted in each site within several 10 cm × 10 cm plots in which the density of seedlings was determined. Relationship between the flowering on time scale and its sites on spatial scale (longitude, latitude, and altitude in this case) was checked by One-way ANOVA analysis. If $P < 0.05$, we assumed that the relationship is strongly. Linear model was adapted to determine the relationship between the duration of the flowering and the altitude of the sites. All calculations were carried out with SPSS for Windows 10.0.

Results

Flowering pattern

Observation carried out in 62 bamboo sites shows that the bamboo plants in 59 sites (95%) completely flowered in 1996–2000. All flowered bamboo plants died off without exception, showing that the flowering of umbrella bamboo is simultaneous (Fig. 2). In 1996, flowering occurred only on the bamboo sites below 2700 m where about 10% (6 of 62) of the bamboo

sites flowered. In 1997–1998, flowering extended up to 2 800 m and bloomed about 39% (24 of 62) of bamboo sites. In 1999, flowering intensively covered all altitudinal ranges and flowered 37% (23 of 62) of the sites. Flowering in 2000 only occurred on the mountaintops above 2 800 m and flowered 10% (6 of 62) of the bamboo sites (Fig. 3).

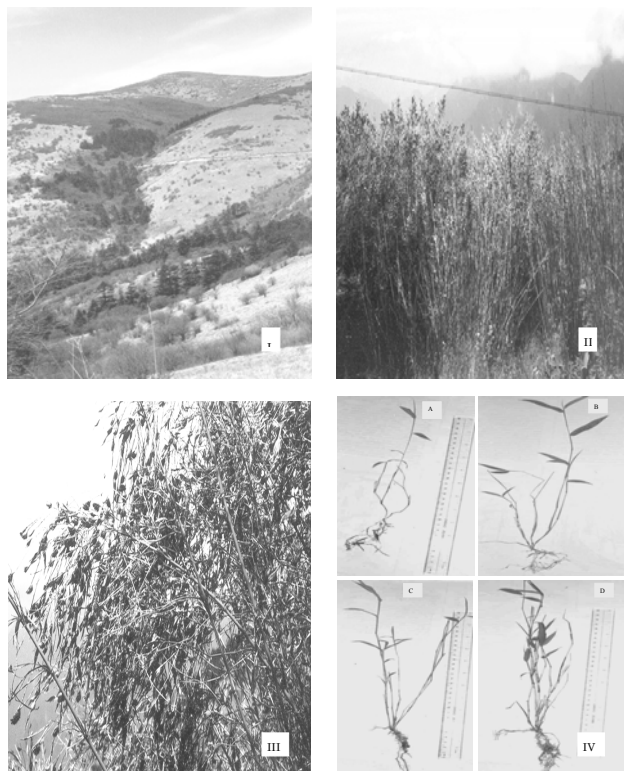


Fig. 2 Flowering of umbrella bamboo (*Fargesia muriei*) on Mount Shennongjia, Central China.

(I) Flowering extent from low elevations (dark thickets on lower slopes) to high mountains (yellowish mosaics on mountaintop) in 1996–2000 (Location: N31°27', E110°16', alt. 2600–3000 m). (II) One clump usually synchronously flowered in one year (left clump flowered in 1999, middle one in 1998, and right one in 1997). (III) Seeded bamboo plants (flowering occurred in April–May, seeds matured in September–October). (IV) Bamboo seedlings. IV(A) Two-year old seedling; IV(B) Three-year old seedling; IV(C) Four-year old seedling; IV(D) Five-year old seedling.

Flowering duration in low elevations was longer than that in high mountains. In the bamboo range below 2 800 m, habitats took four to five years to flower all bamboo sites, while habitats above 2 800 m took only two years (Fig. 3). The relationship between flowering duration and elevation can be described by a linear model: $Y = 18.8 - 0.57X$ ($r^2 = 0.612$, F -value = 6.32, $P < 0.05$), where Y indicates the flowering duration in years and X indicates the altitudinal step in 100 m. Different slopes had different flowering durations: on the northern slopes (Path 1), flowering lasted only three years (1998–2000), while on the southern slopes (Path 2) and mountain ridges (Path 3) it lasted five years.

A one-way ANOVA analysis (Table 1) shows that the flowering of umbrella bamboo tends to extend from lower elevations to the higher mountains along the altitudinal scale ($P < 0.001$), and from southwest to northeast along the mountain settings. Specifically, on the northern slopes (Path 1), flowering signifi-

cantly extended from west to east and approximately from low elevation to higher altitudes ($P < 0.005$), but was not affected by the latitude ($P > 0.05$). On the southern slope (Path 2), flowering strongly related to altitude ($P < 0.001$), latitude ($P < 0.005$), and longitude ($P < 0.001$). However, flowering along the mountain ridge (Path 3) at a similar altitude seems to have no connection with the geographical location ($P > 0.05$, Table 1). This implies that the latitudinal and longitudinal effects may be a topographical influence derived from the geographical setting of the mountains. The associated vegetation did not strongly affect the spatial pattern of the flowering time, since the tree canopy and bamboo cover contributed very little to determining the flowering time (Table 1).

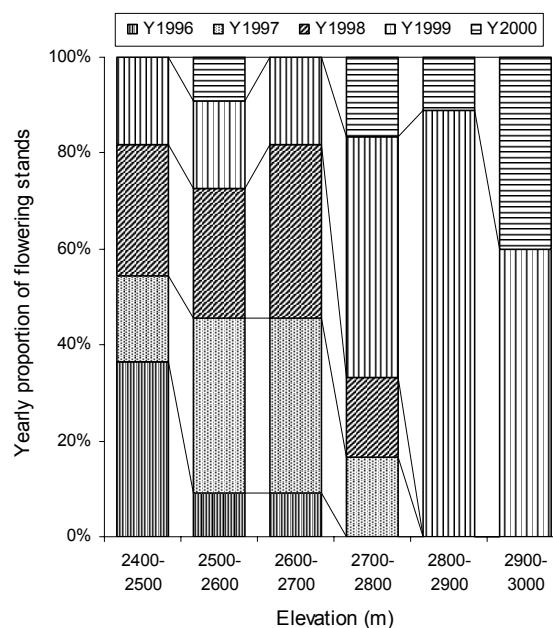


Fig. 3 Altitudinal flowering patterns of *Fargesia muriei* on Mount Shennongjia, Central China.

Bamboo seedling

After simultaneous flowering, the parent clumps die off and the recovery of the bamboo sites totally depends on the establishment and growth of bamboo seedlings. Our investigations show that most of the bamboo seedlings emerged in the year following the simultaneous flowering (Fig. 2-IV). The density of the bamboo seedlings, on an average level, was as high as $5\,460 \pm 4\,800$ (Mean \pm S.D., thereafter) seedlings·m⁻² in the autumn of 2000 in the bamboo sites which flowered in 1999, while that was about $1\,130 \pm 1\,000$ seedlings·m⁻² in the bamboo sites which flowered in 1998. This indicates a high mortality during the first winter. Through 2–4 years of age, the seedling density was seemed relatively stable (Table 2), as the mortality of the older seedlings might be compensated by the newly emerged ones. Although the community structures did not affect the flowering time of underlying bamboo clumps, bamboo coverage tended to positively affect the seedling density ($r = 0.372$, $P < 0.01$), probably due to denser bamboo clumps, which produce more seeds and shade the floor more efficiently. Meanwhile, herb coverage obstructed the seedling density ($r = -0.392$, $P < 0.01$). Seedling density varied from site to site, but strongly related to the associated vegetation types. On average level, the conifer -

bamboo community usually carried the highest seedling density ($3\,980 \pm 4\,750$ seedlings m^2), followed by the pure bamboo community ($2\,490 \pm 2\,470$ seedlings m^2) and the deciduous tree -

bamboo community ($1\,570 \pm 1\,110$ seedlings m^2). Shrub - bamboo and bamboo - meadow communities were relatively poor in bamboo seedlings.

Table 1. Summary of One-way ANOVA analysis on the relationships between flowering year of *Fargesia murielae* and the spatial factors on Mount Shennongjia, Central China. In the table: *d.f.* = degree of freedom, *F* = *F*-value, Sig. = Significance level.

	Path 1			Path 2			Path 3			Over all		
	<i>d.f.</i>	<i>F</i>	Sig.	<i>d.f.</i>	<i>F</i>	Sig.	<i>d.f.</i>	<i>F</i>	Sig.	<i>d.f.</i>	<i>F</i>	Sig.
Geographical effects on flowering time												
Altitude	2,18	4.68	0.026	9,30	15.53	0.000	2,9	0.34	0.841	9,59	10.572	0.000
Latitude	2,18	0.84	0.449	9,30	5.20	0.003	2,9	0.85	0.548	9,59	0.907	0.466
Longitude	2,18	8.06	0.004	9,30	10.13	0.000	2,9	0.16	0.949	9,59	4.790	0.002
Vegetation effects on flowering time												
Canopy	2,18	0.35	0.708	9,30	3.98	0.012	2,9	0.35	0.833	9,59	3.703	0.010
Bamboo	2,18	1.23	0.319	9,30	3.10	0.033	2,9	4.96	0.054	9,59	1.495	0.217
Herb	2,18	0.22	0.804	9,30	2.96	0.038	2,9	1.16	0.425	9,59	2.294	0.071

Table 2. Umbrella bamboo (*Fargesia murielae*) seedling density (seedlings 100 cm^2) in 2000 in the bamboo sites flowered in 1996-1999 on Mount Shennongjia, Central China

Flowering year	1996	1997	1998	1999
Path 1	NA	NA	13.9±11.1	72.8±55.3
Path 2	14.0±4.1	12.8±13.7	11.2±9.1	63.3±41.8
Path 3	2.0±0	6.0±1.4	3.0±0	16.8±30.3
Total	12.0±6.2	12.3±12.3	11.3±10.1	54.6±48.0
CB	15.4±4.1	7±1.4	9.6±7.4	71.1±50.3
DB	10.0±0	NA	19.3±12.3	7.0±0
PB	NA	16.0±13.7	3.0±0	44.0±29.8
SB	NA	3.0±0	NA	NA
BM	2.0±0	NA	3.0±0	2.5±2.1

Discussion

Flowering interval

All *F. murielae* plants in Europe and North America were propagated vegetatively, starting with one plant from Mount Shennongjia. Living plants of umbrella bamboo was firstly sent to Arnold Arboretum (the USA) by E. Wilson in 1910, and then from there a single plant was sent to Kew Gardens (the U. K.) in 1913, where it was propagated (Ohrnberger 1999). The plants at Arnold Arboretum did not survive. Later, the species was re-introduced into the USA from Europe (firstly in 1960 from the Royal Moerheim Nursery, Dedemsvaart, Netherlands). In Europe and North America, the species flowered in 1993–1998 (Eberts 1996; Gielis *et al.* 1999; Shannik 1999). Considering this is the first simultaneous flowering since 1907 when Wilson gave a record to this species (Sargent 1911), its flowering interval was estimated as being about 90 years (Shannik 1999). However, we should be cautious to accept this estimation because this species was introduced in the West as a vegetative clone, rather than as seeds or young seedlings.

In Shennongjia, the local elders indicated that the umbrella bamboo did not simultaneous flower between the “establishment of new China” (the Peoples' Republic of China) in 1949 and 1996, but the elders could not recall the flowering prior to 1949, which left a long gap between 1907 and 1949. In April 1907, Ernest Wilson recorded that this bamboo (specimen *Wilson 1462*, Kew) was “2–4 m tall, stems golden, without flowers” (in Sargent 1911). In 1922 and 1926, the Chinese pioneer botanists H. R.

Cheng and R. Cheng respectively visited Shennongjia; however, they neither recorded nor collected this bamboo species. We assume that the bamboo did not flower when they were there, as they would otherwise have had a flowering collection. The first record of this species in China is probably the vegetative specimen collected by Chang H. Zhou in 1935 (in Herbarium of Wuhan University, named as “*Arundinaria sp.*”). In 1943, another Chinese botanist Zhan Wang visited the umbrella bamboo ranges. His field colleague, the local governor Wen Z. Jia, described the mountaintop of Shennongjia - the distribution center of umbrella bamboo, as “bamboo brush likes a blue sea and dense firs shade the sky; here is the highest peak of Central China” (Cui 1996). It indicates the bamboo did not flower then. Considering the records above and the species did not flower between 1907 and 1996 in Europe, We assume that the umbrella bamboo in Shennongjia presents the same flowering cycle as it performed in Europe and North America. Furthermore, given that the umbrella bamboo was in a full vegetative phase in 1907 (Sargent 1911) and *Fargesia* seedlings need about 20 years to reach such full phase (Taylor and Qin 1993), we estimate that flowering interval of umbrella bamboo may be as long as 110 years, or more.

Flowering pattern

Flowering of the umbrella bamboo on Mount Shennongjia took about five years. However, flowering was not randomly across the habitat: Observations indicate a temporal sequence during the flowering period. On the same slope, higher elevation sites tended to delay and decrease duration of the bamboo flowering (Fig. 2-I). The altitudinal delay of simultaneous flowering is a common phenomenon over the mountain bamboos. Yi (1997) reports that flowering of fountain bamboo (*Fargesia nitida* (Mitford ex Stapf) Keng f. ex Yi) on Mount Jiuzhaigou in West Sichuan from 1982-1985 obviously extended from a lower elevation (started in 1982 below 2 700 m) to the mountaintop (started in 1985 over 2800 m). Taylor *et al.* (1991) recorded that in the Wolong Giant Panda Reserve, West Sichuan, such a delay had led to the survival of *Bashania fangiana* (Camus) P. C. Keng and Wen in high altitude areas (above 3 000 m) for several years.

Cultivated umbrella bamboo also performed a geographical delay in this worldwide flowering process. Genetically, all plants of umbrella bamboo scattered in Europe and North America should flower in the same year because they came from the same

clone; however, the flowering process lasted six years from 1993 to 1998. In Europe, simultaneous flowering started in Germany and Britain, then extended to Switzerland (Eberts 1996; Gielis *et al.* 1999). In North America, flowering started in the USA in 1995, and in Nova Scotia, the flowering was delayed until 1998 (Shannik 1999). It means that the environmental variables may delay the flowering for some years, but may not change the flowering cycle of this species.

Seedling establishment

Makita (1992) divides the early regeneration process of bamboo after simultaneous flowering into three phases: establishment, stable density, and thinning phases. In the life history of bamboos, the seedling is most vulnerable shortly after germination (Young 1985; Taylor and Qin 1988). Our field data (Table 2) show that the seedling population suffered from a high mortality during the first winter after germination. In the conifer-bamboo community, bamboo seedling density fell from 7 110 seedlings·m⁻² in the first year sites to 960 seedlings·m⁻² in the second year sites after flowering, with a possible mortality rate as high as 85%. However, the seedling density was stable in the years 2 to 4, maintaining about 1 130–1 230 seedlings m⁻². This initial result indicates that there is a very high mortality of the one-year old seedlings, but a stable phase between 2 and 4 years. When and how the seedlings pass through the self-thinning phase needs further observation.

The seedling density in two vegetation types, shrub - bamboo and bamboo - meadow communities, showed an average of 200–300 seedlings·m⁻², near that of *Fargesia scabrida* Yi in West Sichuan eight years after the simultaneous flowering (Qin 1985). On Mount Shennongjia, deciduous forest, shrubs and meadow over the bamboo habitats between 2 400 and 3 100 m have long been considered as secondary vegetation of the local climax of the fir (*A. fargesii*) forest (Ban *et al.* 1995). Low seedling density in such secondary communities indicates that human disturbances (i.e., burning and logging) may negatively influence the regeneration of natural bamboo sites. Taylor *et al.* (1993) studied the dynamic of bamboo seedlings of *B. fangiana* in clear-cut and closed forest. Their results suggest that although at first seedlings appeared in both stands after simultaneous flowering, finally the seedlings in a closed forest rebuilt the bamboo community, while the seedlings on clear site lost vigor and were unable to restore the bamboo stand. Further studies are needed to assess whether *F. murielae* follows the same regeneration pattern of *B. fangiana* or not.

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